The Dorsal Vibratile Fin of the Rockling (Motella).

By

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With Plate 11.

Most collectors on our shores are familiar with the rockling, and have observed the series of free, vibrating rays situated slightly anterior to the ordinary dorsal fin. It is the object of the present paper to give an account of this vibratile fin, together with co-related parts, and to indicate its function as a whole.

Bogoljubsky holds that this vibrating fin has not any physiological function other than that of a "lure," which is supposed to act in a somewhat similar manner to the anterior filament in the fishing frog or angler-fish, Lophius piscatorius. This explanation does not appear to me satisfactory, especially as no suggestion is made as to the precise method by which this supposed "lure," situated some distance posterior to the mouth, acts. From the standpoints of morphology and physiology I have come to the conclusion that the part has to be regarded as a highly efficient gustatory or food-detecting and food-locating organ.

The two species of rockling most commonly collected on our shores, and on the bottom in deeper water, are the three-bearded rockling, Motella tricirrata, and the five-bearded rockling, Motella mustela. As regards the habits of these fish, one may notice that they are shy, nocturnal, phlegmatic, non-predaceous, and, as was pointed out by Bateson some years ago, do not, as a rule, seek or find their food by sight. On the sea-shore, the rocklings are mostly found lurking under stones between tide-marks, a large part of their skin being frequently coated with small grains of sand.

In connection with my contention that the vibrating fin is not purely and simply a lure, it is important to notice that the food of the rockling consists of crustaceans such as prawns and gammarids, annelids, star-fish, pycnogons, and even other fish.

The dorsal vibrating fin is very conspicuous, and in the still water of an aquarium its movement may be observed at a distance of three to six feet. The dimensions of the fin naturally vary considerably in specimens of different size. In a large specimen of Motella tricirrata, measuring 260 mm. in length and 95 mm. in girth, the groove in which the vibrating rays are situated was 32 mm. in length, and the large anterior ray was 7 mm. long. The fin is situated a slight distance (about ½ cm.) posterior to the head, and is separated from the ordinary dorsal fin by about an equal interval.

The vibratile fin consists of a series of comparatively small processes, which are almost continuously in rapid vibration, and anterior to these, a ray which is much longer and thicker than the others, and has much less power of movement. The individual rays are connected with one another near the base by a fold of skin, which passes off almost at right angles, and by this arrangement each ray has the power of independent movement. The rays arise medially from the base of a groove, the sides of which are chiefly formed by the lateral myomeres.

The vibration of the rays resembles the movement of cilia, and there is an independent motion of each, and a collective action of groups of rays. A sinuous wave-like vibration is thus produced, which drives currents of water in a latero-posterior direction over the sides of the groove. The movement of the rays or processes is almost constant, although it may, at rare intervals, cease for several seconds, or even a few minutes. This interval of cessation is irregular and non-periodic. When the movement is about to be discontinued, the posterior rays cease first, and then later, those situated more anteriorly. In a similar manner, when the movement is being resumed, the anterior rays come into motion previous to the posterior processes.

In a good light the individual processes can be detected with the naked eye originating from a greyish ridge at the base of the groove, and with a reddish area on either side of the raised part. The anterior ray has only a very slight vibration in a lateral direction, which may be observed with a lens. The movement of the other processes is in a latero-posterior direction. On firmly pressing the surface of the anterior process with a sharp pencil or other small object it becomes depressed, and the movement of the remaining rays ceases, and conversely, on placing pressure on the small processes situated immediately posterior to the large ray, the latter is depressed. This depression of the anterior ray also occurs with fairly firm contact on the posterior processes, but not in such a marked degree. When a thin strip of paper is placed along the posterior surface of the large process, the small rays cease their movement; this means of communication seems localised, for when the paper is placed in contact with the anterior side, the cessation of vibration does not take place. There is thus apparently a certain degree of continuity between the large anterior process and the smaller rays. The small rays or groups of those have, however, the power of independent movement, for on touching certain of them their movement ceases, while those situated anteriorly or posteriorly still have the power of vibrating.

The result of coating the sides of the groove, in which the fin is situated, with black asphaltum, was a cessation of the movement of the vibrating rays for some time, although when the rockling was touched and consequently changed its position the rays recommenced to act; but otherwise the fish appeared curiously inert, almost as if asleep. In half an hour's time a layer of mucus had become deposited on the sides of the groove.

On adding chloroform to the water in which the rockling is living, the movement of the vibratile fin ceases, although the animal freely moves its pectoral fin. Similarly, the addition of cocaine to the water containing a small rockling (2–3 in. in length) has the effect of stopping the movement of the rays for intervals varying from forty seconds to three minutes.

The action of the vibrating processes apparently maintains a clear area of skin on either side of the groove. My experiments, which consisted in letting down granules of carmine by means of a pipette, show that while these grains readily adhere to most parts (probably from the secretion of mucus), yet there remains an area on either side which keeps clear of carmine particles. The absence of carmine particles soon delineates very distinctly the area of vibration from the pigmented skin of the general surface of the body. A similar result evidently occurs when the fish is living in its natural habitat, as I have repeatedly noted that when rocklings are brought in from the shore they have a coating of sand on the general surface of the skin, with the exception of the area immediately surrounding the vibratile fin.

When the vibratile fin ceases movement, the large anterior process is folded backwards over the smaller processes, and these in their turn over those situated more posteriorly.

On lightly touching the sides of the groove, the processes fold themselves down on the opposite side of the groove to that which has been touched.

In the light of my subsequent remarks, it is interesting to notice that contact on the barbules and pelvic fins results in renewed movement of the vibrating rays when this has been stopped, but that the same result does not take place on contact with the pectoral fins. We will later notice that the barbules and pelvic fins have the same general mode of innervation as the area under discussion.

Bogoljubsky coated the rays from the dorsal surface with gelatine and tannin, and even cut them away entirely, without apparently causing any physical discomfort, and without affecting the movements of the fish. He also states that cutting away the rays was subsequently followed by their regeneration. I obtained somewhat similar results so far as regards the fin itself, but I hold that the author has neglected the study of the skin in the immediate proximity of the vibrating rays.

In the course of my work I was early struck by the fact that the skin in the near neighbourhood of the vibrating processes is extremely sensitive; thus, for example, when a thin strip of paper is laid on the sides or apex of the groove bordering the processes, the movement of the latter is brought to a standstill. On the other hand, if the same contact is tried on the dorsal and pectoral fins, or on the surface of the head, the movement of the rays continues uninterruptedly. I will have occasion later on to refer to the occurrence of a number of tactile nerve-endings on the skin of the groove in which the rays are situated.

It is not easy to understand how Bogoljubsky arrived at his conclusion that neither from morphology nor from physiology can one ascribe any physiological rôle to this organ.

The vibratile fin of Motella, which may be termed the oral fin in contrast to the longer dorsal or aboral fin, is comparable in general structure to that of the unpaired dorsal fin of other Gadidae.

In the case of the smaller processes the structure is as follows:

From the spinous process of the vertebra a ray-carrier or radial passes dorsalwards, and at the apex of the latter a small spherical articulating process is situated to which the ray is attached. The radials or ray-carriers have a pillar-like form, differentiated into three parts, namely, a head, neck and base. The ray-carrier consists of hyalin cartilage which is richly impregnated with salts of lime. The individual ray-carriers are connected with one another by ligamentous tissue.

Each of the rays, with the exception of the first, contains two horny fibres which are separated from one another by connective tissue, and approach one another near the base. Each ray has an anterior and posterior basal enlargement. From the anterior of those a muscle passes almost vertically in a ventral direction and attaches itself to the lower part of the ray-carrier. This muscle acts as an erector elevating the ray. On the other hand, from the posterior process, a muscle passes obliquely downwards along the neck of the ray-carrier and fixes itself slightly dorsal to the attachment of the anterior muscle. This muscle acts as a depressor, lowering the processes into the groove.

The form of the first anterior process differs slightly from those just described. It contains only a single horny fibre, which divides at the base, and there are three small, basal processes to which the tendons of muscles are attached. It also differs from the smaller processes in that the ray is more directly connected with the ray-carrier by means of embryonal cartilage.

Transverse sections through the rays near their apexes show an external, many-layered epithelium containing mucous glands; within this a deeply pigmented layer is situated, which surrounds a mass of centrally disposed connective tissue. The latter contains blood-vessels and two horny fibres.

The individual rays are, as previously stated, connected with one another by a fold of skin near the base.

The vibratile fin is supported in its position by means of a ligament, which surrounds and covers the spinous processes of the vertebræ, and dorsally to these also envelopes the centrally situated ray-carriers. This paired ligament takes its origin in the supra-occipital, and it proceeds in a posterior direction on either side of the ray-carriers, but on arriving at the aboral fin the two layers, right and left, unite into one.

The fin is, as previously stated, situated in a groove, whose internal boundaries are chiefly formed by the very prominent lateral myomeres. The walls of this groove more or less protect the rays, especially when these are depressed. While I find myself in essential agreement with the description and figures of the structure of this fin as given by Bogoljubsky (pp. 329–332, figs. 3–7), I must now proceed to important points, more especially in regard to the structure of the surrounding skin, which are not dealt with in his investigations.

Fig. 2 illustrates the structure of the ventral part of the vibratile fin and adjoining parts, as seen in transverse sections. The skin covering the groove in which the fin is situated is scaleless, and its detailed structure is of the greatest importance for the understanding of this organ. The skin consists firstly of a many-layered epidermis, consisting of a series of squamous cells externally, which gradually pass over into more columnar cells internally. Within the latter a deeply pigmented layer is situated. The epidermis also contains numerous mucous glands, and, of more importance, a large number of tactile nerve-endings and terminal or taste-buds. Beneath the epidermis there is a slight space traversed by strands of connective tissue, through which nerve-fibres pass. These strands of connective tissue pass internally into a well-defined layer of compact, ligamentous tissue. Underneath the dermis the large lateral myomeres are situated. The medial and ventral part of the section also contains a mass of connective tissue with two nerves on either side, the larger one being the ramus lateralis accessorius and the smaller one a dorso-spinal nerve. The section also passes through one of the depressor muscles. The medial and dorsal part of the section passes through the skin, which connects the basal part of the rays (the proximal parts of the rays not being included in the sectional plane). The epidermis of this fold of skin is similar in structure to that of the groove. Within the epidermis is a pigmented layer, and internally to the latter is loose connective tissue containing the horny fibres of the rays cut transversely, nerves, and blood-vessels. At the base of this fold of skin the head of the ray-carrier is seen, with embryonal cartilage disposed dorsally to it, and then the articulating sphere for the ray.

The occurrence of numerous terminal or taste-buds ("becherförmigen Organe") in the epidermis of the groove bordering the fin is particularly noteworthy in connection with this investigation. These taste-buds, which project slightly on the surface of the epidermis, are bulb-like organs containing long, sensory cells. The taste-buds have a marginal layer of cells, which form a definite limiting membrane. The sensory cells consist of (1) a long, cylindrical, apical part terminating in a bristle which projects slightly on the surface of the epidermis, (2) an expanded part containing the nucleus, and (3) a basal part, which is continuous into one or more fibres. The taste-buds are also in connection with nerve-fibres.

Bateson has described similar organs on the barbels, pelvic fins and palate of the same fish, and the taste-buds, which I now bring under notice, are similar in structure to those described by him from these other parts.

I have also compared these taste-buds with the "neuromasts" or organs of the lateral line in the rockling, and agree with Herrick in his contrast of gustatory buds and neuromasts. The "neuromasts" are, as a rule, sunk beneath the skin in canals, tubes or pits, while taste-buds are superficial, or may slightly project on the surface. The specific, sensory cells of the neuromasts only extend partly through the space limited by the sensory epithelium, and thus do not reach the internal, limiting membrane; on the other hand, in taste-buds the sensory cells extend from the external to the internal boundaries. The sensory cells of neuromasts frequently end in hairs, and are therefore sometimes termed "hair-cells," while those of taste-buds may terminate in bristles but not in hairs.

A further contrast, which I may now refer to, is the mode of innervation. The vibratile region of the rockling is innervated partly by the ramus lateralis accessorius, and in part by branches of the dorso-spinal nerves. The ramus lateralis accessorius is a recurrent branch of the facial nerve, and belongs to the system known to comparative anatomists as the "communis" system. The ramus lateralis accessorius, which has no connection with the nerve of the lateral line, is paired and takes its origin in the lobus facialis of the myelencephalon. It runs backwards (sending off branches on its way to the barbels and pelvic fin), one on either side of the ligament, which supports the vibratile fin, and in the region of the latter its branches anastomose with the spinal nerves at their ganglia. From this anastomosis the nerve-fibres of the ramus lateralis accessorius are sent along with general cutaneous branches from the spinal ganglia to the skin of the region of the vibratile fin. The main trunks of the ramus lateralis accessorius continue to run in a posterior direction, and at the origin of the second or aboral dorsal fin they rise to a higher level, and those of right and left sides become more widely separated from one another. My results regarding the innervation of taste-buds of the rockling agree with those of Herrick in his investigation of the gustatory organ of Ameiurus. According to Herrick, all "terminal buds" are innervated from a bilobed centre, namely, the gustatory tract or "visceral sensory column" of the brain, those of the mouth being connected with the posterior or vagal lobe by the vagus and glosso-pharyngeal nerves, and those of the skin with the facial lobe by means of the facial nerve.

I may at this point note the contrast that while the "neuromasts" or organs of the lateral line are innervated by the acustico-lateralis nerve taking its origin from the tuberculum acusticum or "somatic sensory column" of the myelencephalon, the terminal buds receive their nerve supply from the "communis" nerves arising from the vagal and facial lobes or visceral sensory column.

One may differentiate three systems of nerve-endings in the skin of fishes, namely: (1) The general, cutaneous nerve-endings innervated from the dorso-spinal roots; (2) the nerve-endings in the "neuromasts" innervated by the acustico-lateralis nerves, and (3) the nerve terminals of taste-buds supplied by the "communis" system of nerves.

My experiments to test the physiological value of the taste-buds consisted in bringing various forms of food into contact with, or into the proximity of the groove surrounding the vibratile fin. I find that it is of the utmost importance in these experiments that the rocklings should, firstly, have become thoroughly habituated to the artificial enviroment of an aquarium. The rocklings are so shy and easily disturbed that when brought in from the shore they are for some time too excited to have any desire for food.

The most successful experiments were made with a fish which had been many months in an aquarium, although with other rocklings which had been a week in captive conditions, similar, though not such satisfactory, results were obtained. A further item to be considered in these experiments is the rockling's hatred of light and of light-coloured surfaces. As the rockling is primarily a night-feeder, I conducted many of my experiments at night, and as showing their sensitiveness to light, it may be remarked that it was found necessary to keep the candle-light in a more or less shaded position. In spite of these hindrances, however, the reflexes or responses obtained were definite and precise.

In my earlier experiments I tried the effects of various extracts of beef. In these I directed a current of fluid beef extract by means of a pipette against the surface of the groove on which the taste-buds are situated. The result of this was a response on the part of the rockling accompanied by a swallowing of the liquid food. As a control experiment I directed a current of sea-water against the same parts, but was unable to detect any response.

Subsequently I tried similar experiments with small pieces of liver, the muscles of crayfish and fish, etc., which were held near the taste-buds by means of a thin wire; the result was that responses were obtained, but not so definite as might be desired. The clearest and most reliable reflexes or reactions were, however, obtained on using living lobworms as the bait. Small, living lobworms or parts of these were gently let down through the water upon the skin of the groove surrounding the fin (the eyes of the rockling being at the same time concealed); a reaction was at once obtained, in which the fish either turned sharply round or rapidly "backed water" and seized the prey. This experiment was repeated again and again, and at intervals by day and night, and the response observed was always clear and definite. The effect of placing the food on the taste-buds was so evident as to be at the same time entertaining. If one lowers the bait until it is in contact with the taste-buds, and then very rapidly withdraws it, the fish responds, and then apparently loses the power of locating the food. In this connection it is interesting to notice that an observer states that one species of rockling rubs or rolls itself about its prey.

In experiments of this nature one must be careful not to ascribe to the physiological action of the taste-buds, reflexes or reactions which might be due to the action of the other sense-organs. As regards the sense of sight, the fish did not in my experiments locate the bait by this means, as in many cases the eyes were covered or concealed.

Regarding the sense of smell, it appeared to me that the reflexes were obtained before the odour of the bait had time to reach the nostrils. In regard to this point one may also refer to the work of Bateson and Herrick. Bateson in the section of his paper which treats of the taste-buds of the pelvic fins and barbels of the rockling, says that the fact that the rockling in which the olfactory organs had been removed, did not pay any attention to food that was not put close to it, tends to show that the taste-buds are of use only in actual contact with the food. Herrick holds that the taste-organs are more efficient than Bateson has supposed, and that the latter author did not sufficiently distinguish between the senses of taste and smell. He holds that Bateson's experiments were insufficient to demonstrate the real efficacy of the taste-buds. Herrick obtained reflexes from a tomcod, *Microgadus tomcod*, in which the olfactory organs had been extirpated; further, by letting down beef extract, which had been previously stained in order that the diffusion currents might be observed, upon the taste-buds of the barbules of Ameiurus, the gustatory reflexes were obtained before the diffusing currents, as marked out by the stained fluid, reached the nostrils.

In regard to the sense of touch, in my experiments it seemed that the best-defined reflexes are obtained when the bait is placed in actual contact with the skin of the area under discussion, and this reaction may be regarded as a gustatory and co-related tactile response. One also, however, obtains well-defined reactions when the food is not actually in contact, but only in the proximity of the taste-buds, and this type of response may be regarded as a purely gustatory reflex.

In experiments, which consisted in using small pieces of cotton-wool instead of morsels of food, I also obtained tactile reflexes in which the fish on the first occasions seized the wool. It appears, however, that contact with cotton-wool is not sufficient to maintain the reflex for any length of time, and that the respective reflexes of taste and touch "can be experimentally isolated by training." As the result of my experiments I am inclined to agree with Herrick, who writes: "The final result seems to be that while the tactile sensation is not sufficient alone to maintain the reflex, the addition of the gustatory element is sufficient, and therefore that the gustatory element is the essential element in setting off the reflex." In an addendum to his valuable paper Herrick after further experimentation arrives at the conclusion with which I agree, that gustatory stimuli by themselves, and apart from the co-related tactile accompaniment, "can be localised in space or have a local sign"; although the response is not so strong and definite as the gustatory plus tactile reflex.

One may, therefore, with Herrick, distinguish four reactions: (1) A vague, seeking reaction, excited by the sense of smell, and consisting in an aimless, circling movement; (2) a quick and definite reaction, consisting in a sharp turn of the body and rapid seizing of the bait, which is obtained when the food is placed in actual contact and is due to the co-related reflexes of touch and taste ; (3) a reaction similar to the last, but not so definite, and which is observed when the food is not actually in contact, but only in the proximity of the taste-buds : this may be regarded as a purely gustatory response; (4) a tactile reaction, to which the fish at first responds, but after repeated experiments and then an interval only reacts in a tentative or inquiring manner, with a deliberate movement.

The main purpose of this paper is to indicate that the vibratile fin of the rockling is morphologically, as indicated by Bogoljubsky, a modified part of the ordinary dorsal fin, and physiologically a part which, together with the adjacent skin, forms a highly efficient food-locating or food-detecting organ.

A general correspondence in structure allows us to deduce that this oral fin is morphologically a modification of the aboral fin. The anterior rays of the aboral agree with those of the oral fin in general structure, and the two fins are directly connected with one another by a ligament, although there is a slight external interval between them.

As regards the physiological side, it has already been noted that the vibration of the rays keeps the skin on either side, on which the taste-buds are situated, clear of sand particles, etc. One has also to remember that internal taste-buds are usually associated, as in mouth, pharynx, gill-chambers, etc., with a current of water. I would also suggest that as the rockling is phlegmatic in its habits, and lives on the shore under stones in more or less still water during at least half its life-time, or on the bottom in deeper water, the advantage of vibrating processes driving currents of water is obvious; this vibration no doubt aids in bringing indications of food. The experiments of Herrick with other fish, showing that these detected the presence of food by means of the taste-buds more quickly in running than in still water, is of interest in this connection.

As regards the belief held by some zoologists that the vibratile fin is a "lure" enticing prey to destruction, I may point out that, apart from the fin's position some distance posterior to the mouth, this would be impossible in certain cases, as the prey either does not possess the power of sight or has only feeble visual power. In other cases it is probable that this part does excite curiosity and arrest attention, and that, by this means, the prey is brought within the sphere of action of the taste-buds. On the other hand, it is evident that as the rocklings lie more or less hidden in the sand, animals may come quite accidentally into the proximity of the terminal buds.

It is not suggested in this paper that external taste-buds are exceptional in fishes, but it is held that the vibratile fin region of the rockling is a localised and specially efficient taste- or food-locating organ.

In terrestrial animals the taste-buds are confined to the lips and mouth cavity, and in this case their function is rather to test than to search for food. On the other hand, the external taste-buds of fishes can be used in locating food, and complex reflexes are associated with this in order to effect the capture of food.

This work has been carried out at the Marine Stations of Millport and Cullercoats, and to the authorities at these institutions I must express my cordial indebtedness. I must also thank Dr. E. J. Allen, of the Marine Biological Station, Plymouth, who kindly sent me some material, and also my colleague, Mr. E. W. Shann, for collecting further specimens while working at Port Erin. To Mr. Walter H. Young, Cullercoats, my thanks are also due for some excellent photographs taken during the progress of my work.

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EXPLANATION OF PLATE 11,

Illustrating Dr. J. Stuart Thomson's paper on "The Dorsal Vibratile Fin of the Rockling (Motella)."

Fig. 1.—Lateral view of Motella showing the dorsal vibratile fin.

Fig. 2.—Dorsal view of Motella showing the vibratile fin.

Fig. 3.—Vertical section of the vibratile fin and adjoining parts. The section passes through the fold of skin which connects the individual rays basally, the upper parts of the rays not being in the plane of section. *ar. sp.* Articulating sphere for the rays. *cn. t.* Connective tissue. *d. sp.* Dorso-spinal nerve branch. *ep.* Epidermis. *em.* Embryonal cartilage. *hd. r.* Head of ray-carrier. *hr. fb.* Horny fibres of the rays. *lig. t.* Ligamentous tissue. *l. m.* Lateral myomeres. *mc. gl.* Mucous glands. *m. dp.* Depressor muscle. *pg. l.* Pigmented layer. *ra. lat. acc.* Ramus lateralis accessorius. *tc.* Tactile nerve-endings. *ta.* Taste-buds.

Fig. 4.—Terminal or taste-bud showing the sensory cells and the limiting membrane.

Fig. 5.—Transverse section through a ray. *e.p.* Epidermis. *pg. l.* Pigmented layer. *cn. t.* Connective tissue. *h. f.* Horny fibres.